

Competition between collembolan species in culture jars

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Little has been written about competitive interactions among various species of collembola. Numerous authors have suggested competitive exclusion of different species as an explanation of rarity of concurrence of some forms, but no direct evidence has been available. In order to approach this problem and also to determine whether or not competitive elimination can occur, we have been raising different species of collembola in controlled cultures for three years. Many of these species are found in nature in the same habitats and represent potential competitors. This paper is a summary of the results we have obtained.

Methods and Materials

We used eleven species of collembola (see lower half Table I) in thirteen different interactions. The species studied cover a wide taxonomic range. *Hypogastrura manubrialis*, *Ceratophysella engadinensis*, and *Xenylla grisea* are all members of the family Hypogastruridae. The first two are similar forms and are sometimes placed in the same genus. The last species is sometimes removed to a different subfamily and has strikingly modified mouthparts. *Sinella caeca*, *S. curviseta*, and *Tomocerus minor* are all members of the family Entomobryidae, the first two belonging to one subfamily and the last mentioned to another. *Isotoma notabilis* and *Folsomia candida* both belong to the Isotomidae, *Sminthurinus quadrimaculatus* and the two species of *Arrhopalites* belong in the suborder Symphypleona and are strikingly different from all the species which are members of the suborder Arthropleona. All cultures were raised in standard $7 \times 8 \frac{1}{2}$ cm. specimen jars with charcoalplaster of Paris substrate. Baker's yeast was the sole food and distilled water was added with each feeding. Food was added in sufficient quantities so that a small amount was left at the time of the next feeding. The initial seeding was done in most cases with five animals per chamber. No attempt at sexing or measuring these animals was made although young adults were normally used. In a few cases twenty animals were used as starting stocks,

but in most cases no significant alteration of results was noted and the five animals stocks permitted better observation of early increases. The difficulty of counting large numbers made counts very inaccurate above two hundred individuals in a single jar. All animals were taken from stock cultures with conditions similar to those of the experiment.

TABLE I
Species Interactions Studied.

	<i>Isotoma notabilis</i>	<i>Folsomia candida</i>	<i>Sinella curviseta</i>	<i>Sinella caeca</i>	<i>Tomocerus minor</i>	<i>Xenylla grisea</i>	<i>Hypogastrura manubrialis</i>	<i>Ceratophysella engadinensis</i>	<i>Arrhopalites dubius</i>	<i>Arrhopalites caecus</i>	<i>Sminthurinus quadrimaculatus</i>	Inter-action result
<i>Isotoma notabilis</i>		1 ↓										
<i>Folsomia candida</i>	A		2 ↓	2 ↓	1 →	1 →	2 →	1 →				
<i>Sinella curviseta</i>		B		3	1 →	1 →						
<i>Sinella caeca</i>		C	D									
<i>Tomocerus minor</i>		E	F									
<i>Xenylla grisea</i>		G	H									
<i>Hypogastrura manubrialis</i>		I							1 ↓	1 ↓		
<i>Ceratophysella engadinensis</i> ...		J										
<i>Arrhopalites dubius</i>							K					
<i>Arrhopalites caecus</i>							L				2 ↓ 1 →	
<i>Sminthurinus quadrimaculatus</i> .										M		

Lower half: Interactions studied with letter designations used in text.

Upper half: Nature of interactions: (1) only one species normally reproduces, or if both breed one dominates from the start; (2) one species dominates at first with second taking over after a time; (3) no clear dominance. Direction of arrows indicates

direction of dominance (i.e. $\begin{array}{|c|c|} \hline B \\ \hline A & 1 \rightarrow \\ \hline \end{array}$ means the interaction is of type 1 and

species A normally dominates; $\begin{array}{|c|c|} \hline 1 \downarrow \\ \hline A & B \\ \hline \end{array}$ means the interaction is of type 1 but either species may dominate).

Results — General Comments

In all our culture work there has been a considerable inexplicable fluctuation in productive success. However, the fact that stock cultures of each of the species observed were reproducing heavily during the period of the experiment allows us to assume that persistent or widespread reproductive failure or diminution is correlated with the experimental conditions. Exceptional situations in which stock culture diminution was occurring are indicated in the text.

In a considerable number of cultures no reproduction occurred. In part this is a result of accidental monosexual cultures, but other factors undoubtedly were important. In addition to these non-reproductive cultures, all cultures showed reproductive depression of all species when maintained much beyond two hundred to three hundred days.

In all of our notations reproduction was indicated any time a sudden jump in numbers occurred. This leads to some inaccuracy due to the masking effect of counterbalancing mortality, and the figures thus obtained would be lower than the actual reproductive rates; however, they do furnish us with a good measure of relative reproductive frequency at densities below two hundred which make up the bulk of our observations. In all of the studies concerned in this paper, scattered cultures either reproduced hugely (two hundred or more) or not at all during any given period. This resulted in a lack of statistically significant differences with analysis of variance; however, when these exceptional results were eliminated, virtually all groups and treatments showed statistically significant differences. This, combined with the repetitive nature of many of the results, leads me to believe that the variations seen here are not random.

Results and Discussions — Specific Interactions

By far the largest series of studies were made at room temperature under normal culture condition of weak illumination or under darkness and constant 14° C temperature. The results of interactions under cave conditions (constant temperature and darkness) were always similar to those under normal culture conditions. Except where otherwise noted it can be assumed that one of these conditions was used. Each of the thirteen interspecific interactions will be described only under the first named species.

Folsomia candida.

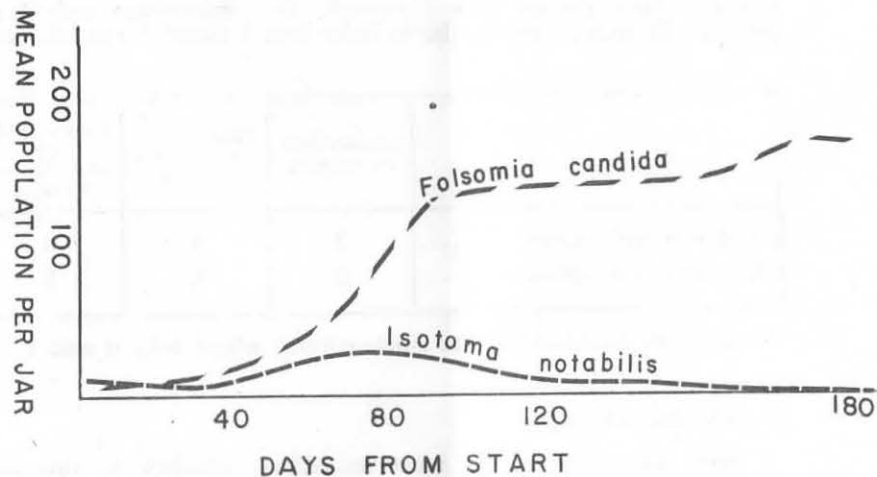
This species is generally a strong competitor and was most widely tested during our study. In three of the seven different interspecific interactions studied, only *Folsomia* reproduced. The table below illustrates these results.

	Cultures with no breeding	Cultures with only <i>Folsomia</i> breeding
<i>Folsomia</i> - <i>Ceratophysella</i> *	2	6
<i>Folsomia</i> - <i>X. grisea</i> *	3	5
<i>Folsomia</i> - <i>T. minor</i> *	2	4

* Taken under varied conditions. See discussion p. 9.

Folsomia candida — *Isotoma notabilis*.

In this interaction, ten cultures were run. In three no breeding occurred, in four only *Folsomia* bred, and in three both bred, but *Folsomia* quickly dominated (see graph 1). In two cases this domination was rapid and resulted in the extinction of *Isotoma*. In the third case the *Isotoma* died out after one hundred seventy days.

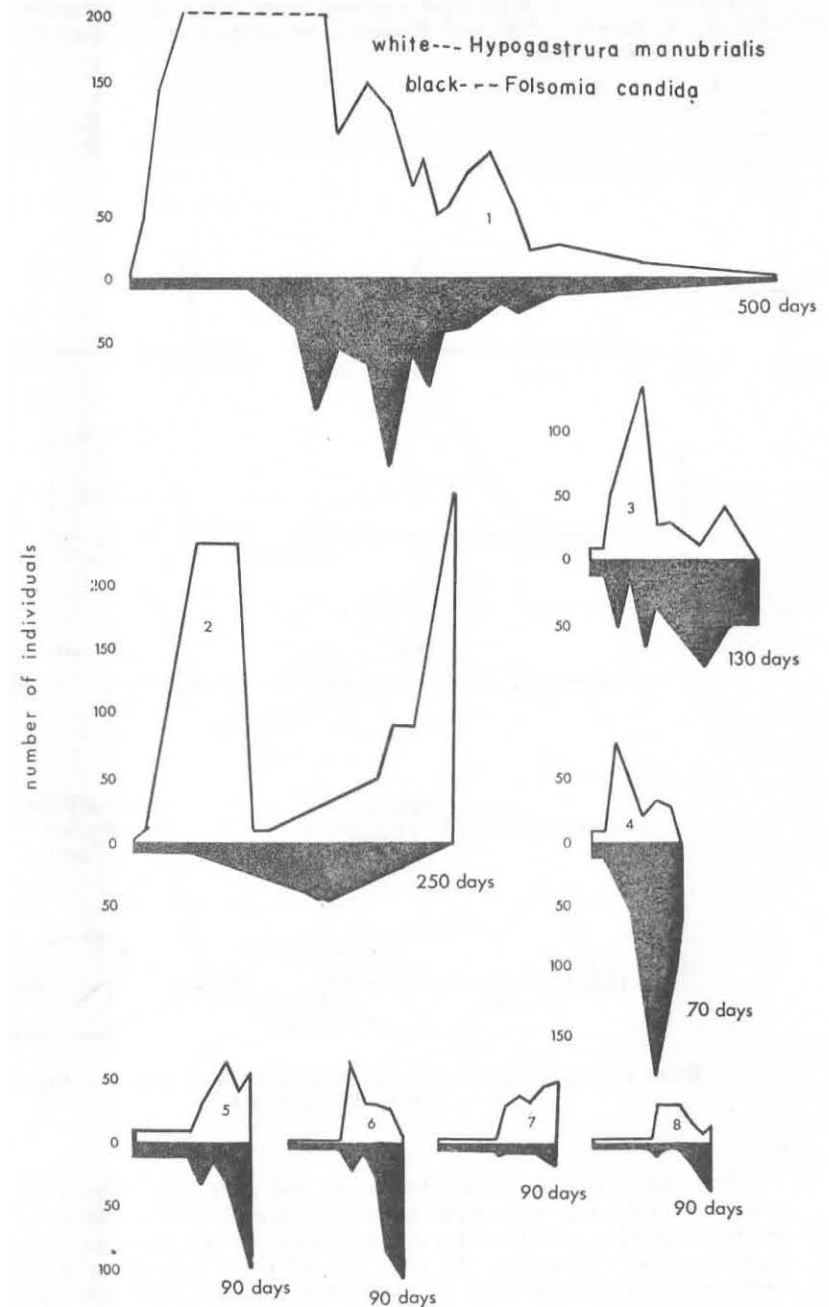


GRAPH 1. — Mean interaction between *Folsomia candida* and *Isotoma notabilis* where both species bred.

F. candida — *Hypogastrura manubrialis*.

This interaction was much more complex and varied. Fifteen cultures were run with this combination, in three series. In none of these was there no breeding, reflecting the fact that both species are good reproducers. In four only *Hypogastrura* bred, while in one only *Folsomia* bred. In ten of the cultures both species bred. In one of these *Folsomia* dominated from the start with *Hypogastrura* never exceeding twenty. In another culture the reverse was true and *Folsomia* never exceeded twelve in number. In the remaining eight cultures (see graph 2) *Hypogastrura* started off dominating, but in five of these eight cultures (cultures 3-6 and 8) *Folsomia* eventually took over and in three cases entirely eliminated *Hypogastrura*. Culture 7 might have done the same except for its early termination.

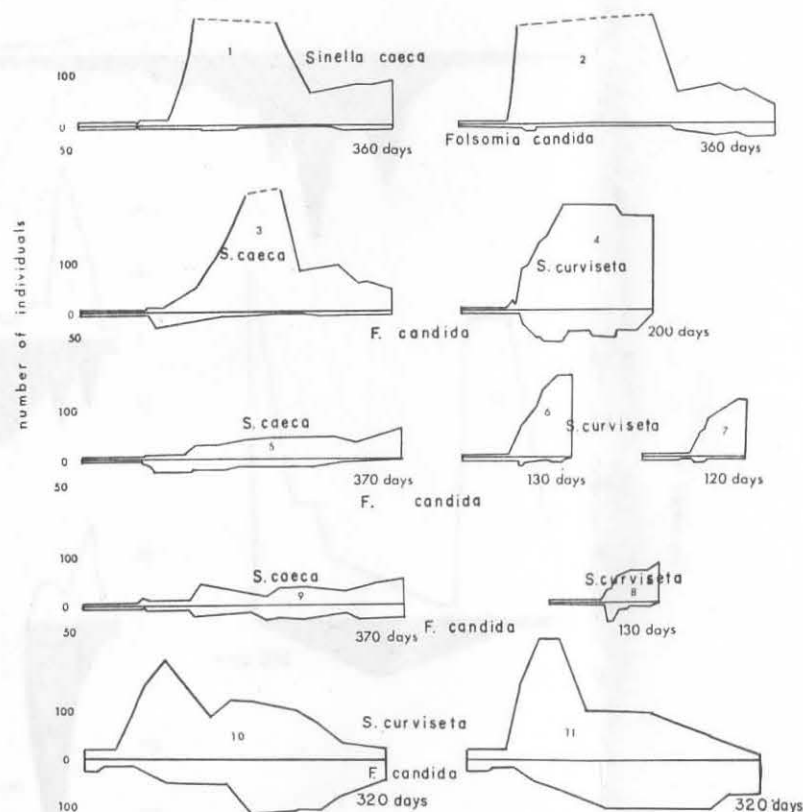
COMPETITION BETWEEN COLLEMBOLAN SPECIES IN CULTURE JARS



GRAPH 2. — Interactions between *Hypogastrura manubrialis* and *Folsomia candida* where both species bred.

The two remaining cultures were unusual in the huge initial reproduction in *Hypogastrura*. No large reproduction took place in *Folsomia* until well after the one-hundredth day, and *Folsomia* never took over as dominant except for a brief time in culture 1.

To summarize, *Hypogastrura* was in most cases the initial dominant form, but normally *Folsomia* built up in numbers past fifty in the first ninety days and went on to dominate. When its build-up past this number was delayed, *Hypogastrura* maintained dominance.



GRAPH 3. — Interactions between *Sinella curviseta* or *S. caeca* and *Folsomia candida* where both species bred.

Folsomia candida — *Sinella caeca* and *curviseta*. The next series of interactions of *Folsomia* were with *Sinella caeca* and *Sinella curviseta*. These were so similar that they will be discussed together. In all, twenty-one cultures were run under normal conditions. In only two of these was there no breeding. In one culture only *Folsomia* bred, whereas seven cultures had only *Sinella* breeding. In eleven cultures under normal conditions both species bred (see graph 3). Essentially two series of results were obtained. In eight of these eleven cases (cultures 1-8) *Sinella* started off dominating and *Folsomia* went further than thirty animals in only one case (culture 4). In three cases (see graph 3) *Sinella* again started

off dominating, but *Folsomia* persisted and started to breed actively between the fiftieth and one-hundredth day and came to dominate slightly in two cases after the two-hundredth day. In this interaction, onset of breeding appears to have little importance, but it does appear that the one hundredth through one hundred and thirtieth day interval is critical for *Folsomia*. In the cultures 9, 10, and 11, where this species made its best showing, there was a substantial reproduction during this period, whereas there was little or none in six of the eight losing cultures. Five of the cultures described above (all involving *S. curviseta*) were started with twenty rather than five animals of each species. In three cases only *Sinella* bred and the other two (cultures 10-11) were two where *Folsomia* was most successful. This larger initial stock left a larger number of *Folsomia* during the critical period.

In summary then, *Sinella caeca* and *Sinella curviseta* both appear to inhibit reproduction in *Folsomia*, but if a sufficient population of *Folsomia* survives beyond the hundred and thirtieth day, this species will increase in percentage as the cultures age.

Sinella curviseta.

Four interspecific interactions were tested with this species. The results with *Folsomia* have already been discussed. The interactions with *Tomocerus minor* and *Xenylla grisea* were similar to those seen between *F. candida* and these species.

	Cultures with no breeding	Cultures with only <i>curviseta</i> breeding	Cultures with only other species breeding	Cultures with both breeding
<i>S. curviseta</i> - <i>T. minor</i>	2	4	0	0
<i>S. curviseta</i> - <i>X. grisea</i>	2	8	1	1

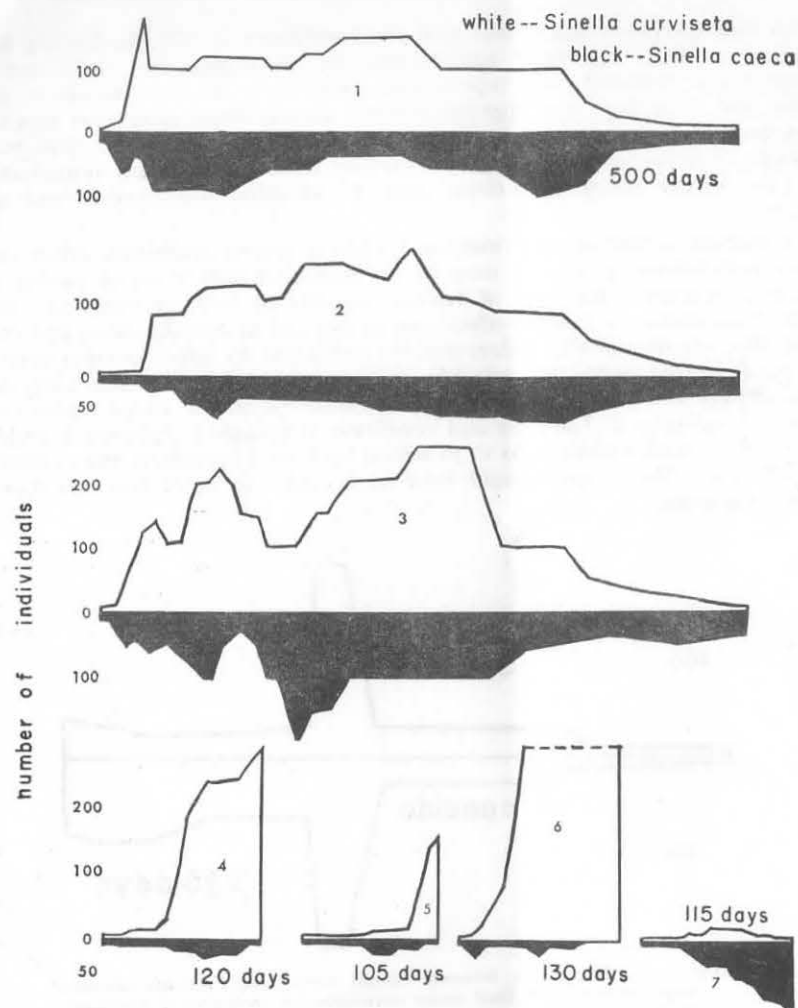
S. curviseta dominated in the single culture where both it and *X. grisea* bred.

S. curviseta — *S. caeca*.

This interaction is the most interesting obtained in this study. The two species are very similar and have similar competitive abilities when compared to *Folsomia*. Twelve cultures were made. In only one case was there no breeding. The remaining eleven cases were distributed as follows: in two cases only *caeca* bred, in two only *curviseta* bred. In three cultures where both bred, *curviseta* eventually dominated, on one *caeca* eventually dominated, and in three neither species fully dominated. (see graph 4). All three of these last cultures behaved very similarly. In one case *caeca* had a brief period of dominance (days 145-160), but otherwise there was an initial dominance of *caeca* followed by a mild, but not striking dominance of *curviseta*, and finally both species deteriorated as the cultures became more than a year old. At the end of five hundred days the terminal figures in these three cultures were:

<i>caeca</i>	<i>curviseta</i>
15	7
25	12
35	6

Considering the data shown here and in graph four, it is probable that these species could live together indefinitely in suitable mixed cultures.



GRAPH 4. — Interactions between *Sinella curviseta* and *S. caeca* where both species bred.

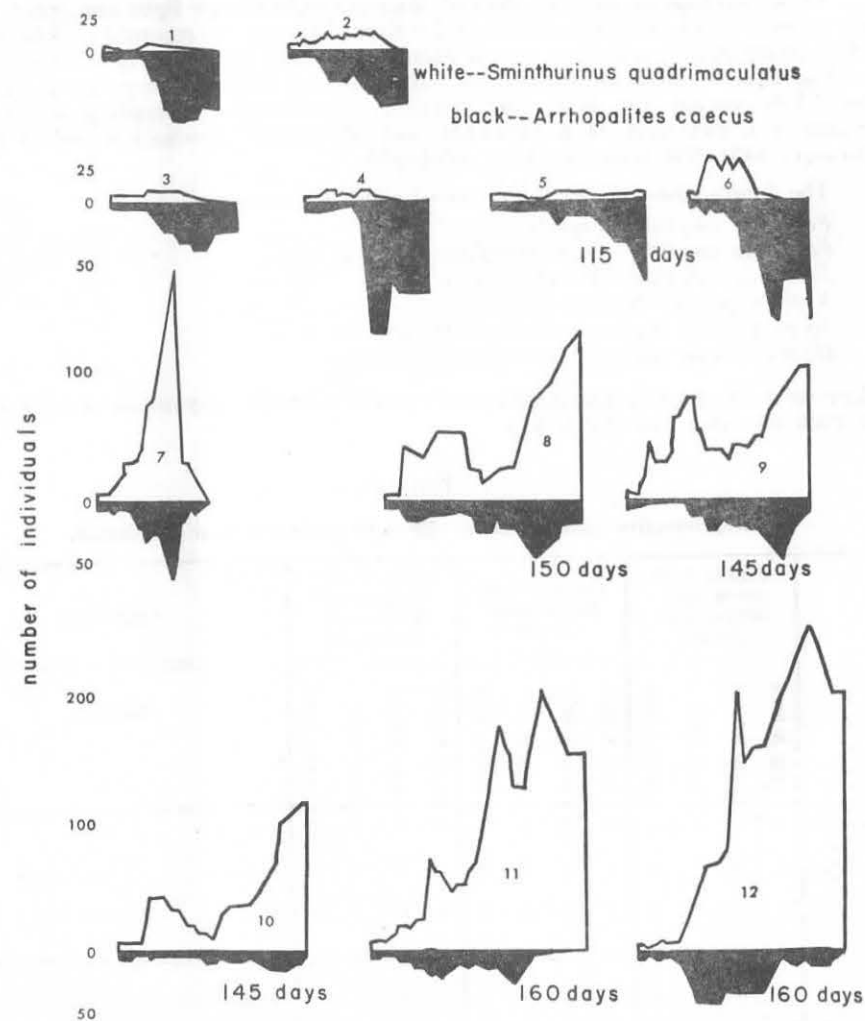
Hypogastrura manubrialis—*Arrhopalites caecus* or *A. dubius*.

The interaction between *H. manubrialis* and *Folsomia* has already been described. The only other species interactions were with two species of *Arrhopalites*. Under culture room or constant conditions the basic reaction was the same for both species. Sixteen cultures were tried, and in four there was no breeding, in nine only *Hypogastrura* bred, while in two only *Arrhopalites* bred, and in one both bred. From the fact that *Arrhopalites* reproduced in only 3/16 of the cultures it would appear probable that *Hypogastrura* has a strong inhibitory effect on reproduction in *Arrhopalites*. The fact that *Hypogastrura* reproduced in 10/16 as compared to 14/15 when in interaction with *Folsomia* gives a less clear indication of a mutual inhibition.

Arrhopalites caecus—*Sminthurinus quadrimaculatus*.

The interaction of *A. caecus* with *Hyp. matura* has just been described. A second interaction, with *Sminthurinus quadrimaculatus* was tested with fourteen cultures. In two there was no breeding, and in all the rest both species bred with two types of results. In six cases *Arrhopalites* dominated and *Sminthurinus* eventually became extinct (see graph 5). In five of these (cultures 1-5) the population of *Sminthurinus* was always very low (fewer than ten) but the remaining instance (culture 6) was anomalous with *Sminthurinus*, building up to thirty in the first thirty days and then plummeting to four animals between days 42 and 46, and disappearing by day 53. Some accidental poisoning might explain this result.

The other six cultures (7-12) followed a very different pattern with both species reproducing during the first sixty days. In some cases *Arrhopalites* domin-



GRAPH 5. — Interactions between *Sminthurinus quadrimaculatus* and *Arrhopalites caecus* where both species bred. All cultures lasting 90 days except where otherwise noted.

ated these cultures during this period, but generally *Sminthurinus* was the more vigorous. Eventually *Sminthurinus* came to dominate strongly in all cases, and *Arrhopalites* either became extinct or very reduced in numbers. This interaction then appears at first to favor *Arrhopalites* overall, but if *Sminthurinus* manages to build up any significant numbers during the early stages it goes on to dominate the culture.

The interactions of *Xenylla grisea*, *Isotoma notabilis*, *Sinella caeca*, *Ceratophysella engadinensis*, *Sminthurinus quadrimaculatus*, *Arrhopalites dubius*, and *Tomocerus minor* were limited to those which have already been described.

Effect of Varied Conditions

In an attempt to see the effect of altered conditions of light and temperature, six species interactions were tried under four different environments. These were: (A) culture room conditions (weak illumination and temperature irregularly fluctuating 20-26° Centigrade), (B) dark with constant 12-13° C temperature, (C) dark constantly except for brief light during examination, fluctuating temperature cycled 24° C 6AM-6PM, 14° C 6PM-6AM, and (D) strong illumination and 24° C temperature 6AM-6PM, dark and 14° C 6PM-6AM.

The interactions tested under these conditions were:

Folsomia candida - *Sinella caeca*
Folsomia candida - *Ceratophysella engadinensis*
Folsomia candida - *Xenylla grisea*
Xenylla grisea - *Sinella curviseta*
Hypogastrura matura - *Arrhopalites dubius*
Hypogastrura matura - *Arrhopalites caecus*

Four cultures of each interaction were started with five specimens of each species in each chamber (see Table II).

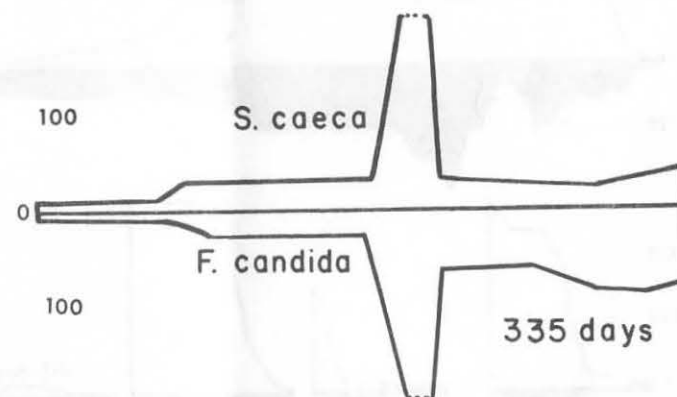
TABLE II

Reproductive success under different environmental conditions.

Results in numbers of cultures	Culture room (weak light, temperature 20°-26°)				Constant dark Temperature 12°-13°				Constant dark Temperature 12 hrs. 24° 12 hrs. 14°				Conditions	
	only X bred	only Y bred	both bred	neither bred	only X bred	only Y bred	both bred	neither bred	only X bred	only Y bred	both bred	neither bred	X	Y
0	1	3	0	0	0	1	2	1	0	0	1	3	<i>Folsomia</i>	<i>S. caeca.</i>
3	0	0	1	4	0	0	0	1	0	0	0	3	<i>Folsomia</i>	<i>Ceratophysella.</i>
2	0	0	2	3	0	0	1	1	0	0	0	3	<i>Folsomia</i>	<i>Xenylla grisea.</i>
2	1	1	0	4	0	0	0	2	0	0	0	2	<i>S. curviseta</i>	<i>Xenylla grisea.</i>
3	0	0	1	3	0	0	1	3	1	0	0	0	<i>Hypogastrura</i>	<i>Arrhopalites dubius.</i>
3	0	0	1	1	1	1	1	0	4	0	0	0	<i>Hypogastrura</i>	<i>Arrhopalites caecus.</i>

The first discovery made was that the conditions in (D) (fluctuating light and temperature) were extremely unfavorable to all organisms. Only one species (*Hypogastrura matura*) had reproduced extensively in this situation after six months, and even here the organisms were mostly dead after two months. For this reason these conditions were abandoned after six months. The remaining conditions in order of decreasing favorability were (A) constant temperature and light, (B) culture room conditions, and (C) variable temperature and constant darkness.

Fluctuating temperature (condition C) has a strong inhibitory effect on reproduction in *Folsomia*, as can be seen by the fact that only three of twelve cultures reproduced whereas eight out of twelve reproduced both in room (A) and constant (B) conditions. A similar effect can be noticed in *Sinella caeca* and *curviseta*. Beyond this, environmental differences do not seem to affect competitive results involving *Folsomia*, with the possible exception of the interaction with *S. caeca*. If we compare the similar interactions of *Folsomia* and *S. caeca* under condition A (graph 3, cultures 2, 3 and 5) and condition B (graph 3, cultures 1 and 9) with the one culture under conditions C, in which both bred (graph 6), the results appear quite different. More work would have to be done to determine whether this is a chance variation.



GRAPH 6. — Interaction between *Sinella caeca* and *Folsomia candida* where both species bred under environmental conditions C (constant dark and fluctuating temperature).

The case of *Xenylla grisea* - *S. curviseta* is quite doubtful. *Xenylla* bred only in conditions A, but the generally low reproduction of *Xenylla* under all competitive cultures leaves great possibility that this is a chance phenomenon. In light of all the results of these first four interactions we can say that evidence exists that strong fluctuating conditions of temperature have an inhibitory effect upon the reproduction of *Sinella caeca*, *S. curviseta*, and *Folsomia candida*, but, with one possible exception, none of those conditions significantly alters the competitive interactions.

The last two series both involve *Hypogastrura manubrialis* and species of *Arrhopalites*. *A. dubius* is a form known so far only from caves, but is closely allied to the troglophile *A. pygmaeus*. *A. caecus* is widely distributed both on the surface and in caves. Under both sets of relatively constant conditions *Hypogastrura* appears to have a clear advantage over both species of *Arrhopalites*. In seven cases only *Hypogastrura* bred, in one both bred, and in one only *A. caecus* bred. If these two are lumped together we get the following results:

Arrhopalites vs. *Hypogastrura manubrialis* - Conditions A, B.

No reproduction	4
<i>Hypogastrura</i> reproduces only	10
<i>Arrhopalites</i> reproduces only	1
Both reproduce	1

The result under fluctuating temperature and constant dark (C) is strikingly different:

No reproduction	0
<i>Hypogastrura</i> reproduces only	3
<i>Arrhopalites</i> reproduces only	5
Both reproduce	0

In this case the indication is that the conditions of strongly fluctuating temperature in constant dark have reversed the normal competitive interaction between the two species.

General Discussion

The results described above, in my opinion, indicate first that there are inhibitory actions of one species of collembola upon another. Among those we have studied, these can be grouped into three large categories:

1) One species generally inhibits all reproduction of the second species, and if reproduction does occur, it is soon successful. Such interactions are indicated by + in the table below.

WINNER

LOSER	<i>Folsomia candida</i>	<i>Sinella curviseta</i>	<i>Hypogastrura matura</i>
<i>Tomocerus minor</i>	+	+	
<i>Xenylla grisea</i>	+	+	
<i>Isotoma notabilis</i>	+		
<i>Arrhopalites</i>			+
(two species)			(only under normal conditions)
<i>Ceratophysella engadinensis</i>	+		

In the two interactions involving *Tomocerus minor* and the one involving *Ceratophysella* the total failure of breeding was associated with irregularity of reproduction in stock cultures and hence these results must remain doubtful.

2) In two interactions, *Hypogastrura* versus *Folsomia* and *Arrhopalites* versus *Sminthurinus*, the first named species dominates at first, but if suffi-

cient numbers are maintained it is later replaced by the second. In the case of *Sinella caeca* or *S. curviseta* versus *Folsomia*, the first two species normally dominate, but if *Folsomia* persists in moderate numbers beyond the one hundredth day, it may increase or even dominate as the culture ages.

3) The last type of result is seen in the interaction between *Sinella caeca* and *S. curviseta* where there is no clear dominance and indefinite co-existence can occur. All of these interactions are summarized in the upper portion of Table I

Irregular and Indeterminate Results

In the various experiments described here there are varying levels of regularity of results. In interactions A, E, F, G, and I (see Table I) the results are always essentially the same. It should be noted that in all cases

	In competition with					
	Isotoma notabilis	Sinella curviseta	Sinella caeca	Tomocerus minor	Xenylla grisea	Hypogas- trura manubrialis
Cultures with <i>Folsomia candida</i> breeding	11	7	5	4	5	11
Total cultures attempted	16	11	8	6	8	16
	Folsomia candida	Sinella caeca	Tomocerus minor	Xenylla grisea		
Cultures with <i>Sinella curviseta</i> breeding	10	9	4	7		
Total cultures attempted	11	12	6	8		
	Folsomia candida	Arrhopa- lites caecus	Arrhopa- lites dubius			
Cultures with <i>Hypogastrura manubrialis</i> breeding	14	5	5			
Total cultures attempted	15	8	8			

Ratio of breeding to total cultures attempted under normal conditions.

save A, the result was a total inhibition of reproduction and in all cases relatively few cultures were examined. In all other interactions there was more or less variability in results. Such indeterminacy has been noted by Lerner and Dempster in 1962 in work with *Tribolium*, and Dawson and Lerner in 1962 have established that genetic variability is the underlying cause. Since the stock cultures from which these experimental animals are derived are not genetically controlled, it is quite possible that this offers an explanation for much of this variability. Pimentel showed in 1965 that reversal of interactions in Diptera, similar in some respects to those seen in our interactions L and M, was the result of a selective change in genotype. The speed with which these reversals can occur in our cultures make this seem improbable, but this could be readily established by further experimentation.

A different type of irregularity occurs in the proportion of reproducing cultures to total cultures made. The preceding table shows these proportions for various interactions. In most cases such as those seen in interactions between *Arrhopalites* and *Hypogastrura*, striking differences can be seen which are explicable on grounds of inhibitory interactions. Most surprising is the consistency seen in *Folsomia*, where regardless of the losing or winning nature of the interaction, the proportion of reproducing to non-reproducing colonies remains constant. At first this would seem to be explicable on the grounds of the chance of obtaining reproductive males and females with a random sample of five animals; however this does not appear to be the explanation. Nine of the interspecific interactions involving *Folsomia* were started with twenty rather than five animals of each species and in these cultures (involving three different competitor species) the proportion of successful cultures was 5/9, almost identical to the typical 2/3 success. Work is being pursued on this puzzling result.

Effect of Competitor Numbers

In species interaction where one form quickly or inevitably dominates another, it appears that no reproduction in the losing species can occur if the numbers of the winner exceed some certain density. In interactions where both species commonly reproduce, there does not appear to be any simple absolute number which prevents reproduction in either species (see graphs 2, 3, and 4). However, when all data is lumped, a clear inhibitory effect of increased numbers of one species on reproduction in be seen (see Table III). This table analyzes changes in three one species when the competing species increases in density or when the species itself increases in density. It shows A) the mean number of young produced per reproduction (recruitment). This parameter is obtained by taking the starting date of each reproduction as the point where young first appear and then including in the figure all the specimens which appear as gradual increases within the subsequent ten days. It also shows B) the mean number of reproductions per one hundred days during which the cultures were exposed to competitor densities of the level indicated, and C) the average total productivity ($A \times B$) during each one hundred day interval. These

TABLE III

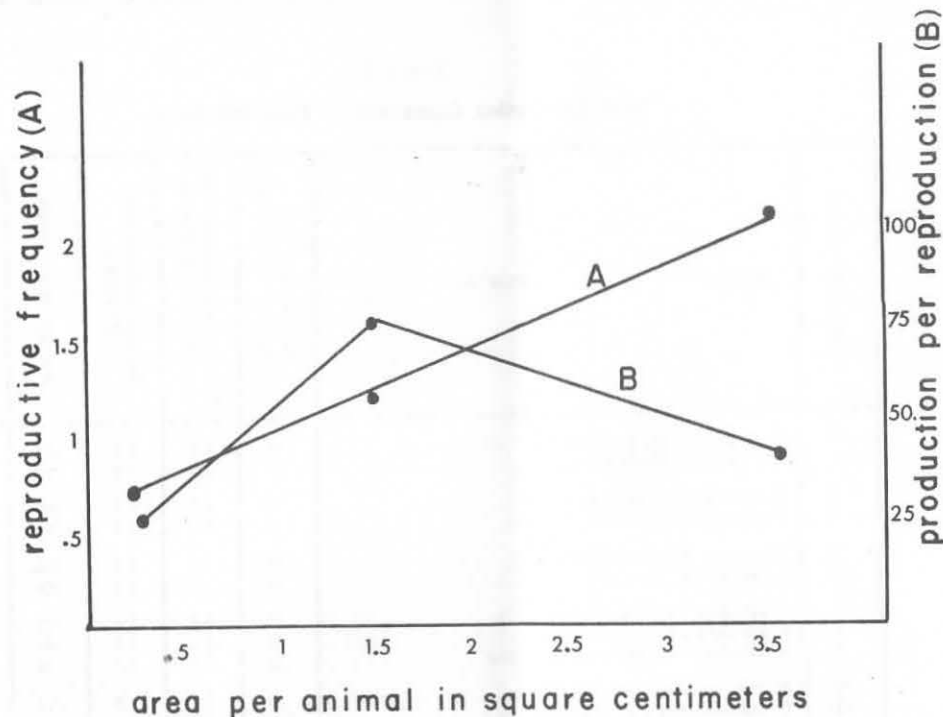
Effect of density on reproduction.

- A) Mean number young per reproduction (recruitment).
B) Mean no. reproductions per 100 days (reproductive rate).
C) $A \times B$ (productivity).

No. OF COMPETITORS IN JAR		0-25	26-100	100	COMPETITOR
Species Being Measured					
1) <i>Arrhopalites caecus</i> .	A (recruitment)	38	45	1	No competition. Self treated as competitor species.
	B (reproductive rate)	2.3	3.4	0	
	C (productivity)	87	153	0	
2) <i>Arrhopalites caecus</i> .	A (recruitment)	13	10	9	<i>Sminthurinus quadrimaculatus</i> .
	B (reproductive rate)	9.9	3.3	1.5	
	C (productivity)	129	33	14	
3) <i>Sinella curviseta</i> ..	A (recruitment)	59	81	48	No competition. Self treated as competitor species.
	B (reproductive rate)	2.4	2.8	0.8	
	C (productivity)	142.0	227	38	
4) <i>Sinella curviseta</i> ..	A (recruitment)	71	50	62*	<i>Sinella caeca</i> .
	B (reproductive rate)	5.6	3.1	7.4*	
	C (productivity)	398	155	459*	
5) <i>Folsomia candida</i> ..	A (recruitment)	47	77	45	No competition. Self treated as competitor species.
	B (reproductive rate)	2.1	1.2	0.8	
	C (productivity)	99	92	36	
6) <i>Folsomia candida</i> ..	A (recruitment)	53	40	43	<i>Hypogastrura manubrialis</i> .
	B (reproductive rate)	3.1	3.7	1.2	
	C (productivity)	164	148	52	
7) <i>Folsomia candida</i> ..	A (recruitment)	23	15	16	<i>Sinella curviseta</i> or <i>Sinella caeca</i> .
	B (reproductive rate)	1.8	0.9	1.3	
	C (productivity)	41	14	21	
8) <i>Sinella caeca</i>	A (recruitment)	37	37	23*	No competition. Self treated as competitor species.
	B (reproductive rate)	2.7	4.4	0.5*	
	C (productivity)	100	163	12*	
9) <i>Sinella caeca</i>	A (recruitment)	18	15	21	<i>Sinella curviseta</i> .
	B (reproductive rate)	19.0	2.8	3.0	
	C (productivity)	342	42	62	
10) <i>Hypogastrura manubrialis</i>	A (recruitment)	63	89	88-	No competition. Self treated as competitor species.
	B (reproductive rate)	2.4	1.4	1.4	
	C (productivity)	151	125	123	
11) <i>Hypogastrura manubrialis</i>	A (recruitment)	109	95	50*	<i>Folsomia candida</i> .
	B (reproductive rate)	3.6	1.3	0.9	
	C (productivity)	392	124	45*	

* Not trustworthy, sample too small.

figures are shown for cultures where both species reproduced and for cultures where only one species ever reproduced and this species was thus in competition only with itself. In all interspecific competitive interaction, increasing density of one of the two species, at least within the twenty-six to one hundred range, is associated with lowered productivity in the other. Comparing interspecific competitive interactions 2, 4, and 9 with the equivalent figures for interactions 1, 3, and 8, where no significant numbers of other species are present, shows that increasing numbers of a second species results in the lowering of both recruitment and reproduction rate, in contrast to the raising of both these parameters in monospecific * cultures of increased density.



GRAPH 7. — Relationships between the area available per animals and: A) mean number of reproductions per hundred days or reproductive frequency; B) mean number of young produced per reproduction or recruitment. *Folsomia candida* in monospecific cultures.

In interaction 7, the lowering of reproductive rate and productivity is again in contrast to the situation seen in monospecific interaction 5. Thus the effect of increased competitor numbers cannot be explained merely as the effect of increased density of animals. In one case, interaction 6, it appears that increasing competitor numbers results in an increased repro-

* Here and elsewhere the term monospecific will be applied to cultures in which there were never more than five animals of any other species present during the life of the culture.

ductive frequency; however, this is not sufficient to counterbalance the lowered number per reproduction and the result is a lowered total productivity. Densities of a second species or competitor of less than twenty-five are generally associated with productivities higher than those seen in similar monospecific cultures. This does not appear to be associated with the optimum density of the species in question. Green, in 1964, has clearly shown that there is an optimum density for *Folsomia candida* reproduction. If we consider that the reproductive frequency in our experiments is a reflection of the proportion of animals with open genital pores, and the average number per reproduction a reflection of Green's figures of fecundity, our data shows a good agreement with his (see graph 7). Our data on all species indicates that all save *Hypogastrura manubrialis* and *F. candida* have maximum productivity in the twenty-six to one hundred density range. Since this level is more common where competitive densities are above twenty-five rather than below, this (see graphs 2, 3, and 4) would indicate a higher than normal productivity at low competitor levels.

In summary, then, increased competitor numbers lowers productivity in all species. In most interactions this is in strong contrast to the effect of buildup of numbers in monospecific cultures.

Comparison with Field Densities

In our most crowded cultures, the total culture surface available per unit animal surface was as low as 1/20; however, most of our significant results were obtained at densities of from 1/1 500 to 1/150. These figures fall into the range of natural densities found by Haarlov in 1960.

Inhibitory Mechanisms

Certain factors can be readily eliminated as important elements in competition. Predation has never been recorded in any of the species used in this study. Food was always in excess of actual consumption; however, in dense populations feeding interference was possible. At the twenty-five to one hundred range of densities where the most striking effects were to be seen, it is extremely improbable that any such effect occurred. The food was scattered and many particles were always available for feeding. Four possible methods of inhibition were considered. These are: 1) destruction of spermatophores, 2) egg destruction, 3) inhibition of oviposition or egg formation, and 4) toxification of substrate with resultant death of young or adults. If we consider that at the lower reproduction rates which make up the bulk of our observations, one reproduction represents egg laying by one or a few individuals, then we can predict how the different competitive mechanisms should affect different aspects of reproduction. To aid this analysis, four measures were developed from our data. These figures were: 1) the

mean number produced per reproduction; 2) the average reproductive rate

$$\sum \left(\frac{\text{No. animals produced}}{\frac{\text{No. present 10 days before}}{\text{No. cultures active}}} \right)$$

3) reproductive frequency

$$\sum \left(\frac{N \text{ reproductions}}{N \text{ active cultures}} \right)$$

If a culture was active for only a part of the time interval being considered, it was entered as a corresponding fraction. The last parameter was

4) Average productivity

$$\sum \left(\frac{\text{young produced}}{N \text{ active cultures}} \right)$$

These figures were obtained for different time intervals from the start of the cultures. Table IV shows the probable effect of each of the earlier discussed inhibitory mechanisms on each of these parameters as well as the total productivity. Destruction of spermatophore should diminish the

TABLE IV

Predicted Differing Effects of Different Competitive Mechanisms.

COMPETITIVE MECHANISM	NO. OFFSPRING PER REPRODUCTION	REPRODUCTIVE RATE	REPRODUCTIVE FREQUENCY	PRODUCTIVITY
Destruction of spermatophores	0	—	—	—
Egg eating	—	—	0	—
Inhibition of oviposition	—	—	+	0
Toxification of substrate with loss of young ..	0	0	—	—
Poor survival of post mature adults	0	0	—	—

chance of fertilization, but once this happens it should not effect the number of offspring produced. Thus this should lower the reproductive rate and frequency, but not the number of offspring produced per reproduction. Any factor such as oophagy resulting in egg loss between laying and hatching should affect both the reproductive rate and the number of offspring per reproduction, but should leave the number of reproductions unaffected since

it is unlikely that all the eggs of a batch would be destroyed. Inhibition of oviposition could either affect all aspects of reproduction or, if it merely resulted in interference with oviposition, affect only the number of eggs produced at one time. In this case there would probably be a compensatory increase in oviposition frequency and no overall reduction in productivity. Toxification of the substrate should affect the number of reproductions and total reproductivity by reducing survival of young to maturity, but should not affect either of the other measures. Toxification should also produce a population development curve with numerous sudden drops. In all cases of concern we have controls in the form of populations where no competition existed. If the results of reproduction in these are compared to joint cultures where competitor numbers exceeded the minimal twenty-five, differences are justifiably ascribed to the effect of competition. Table V sum-

TABLE V

Total Interaction Comparison - First 200 Days.

Interaction number	Species	Competitor	Average no. per reproduction (recruitment)	Average reproduction rate in colonies reproducing	Average reproductive frequency	Average productivity	Interaction number
1	<i>Arr. caecus</i> - no competition		40	6.0	2.9	116	1
2	<i>Arr. caecus</i> - <i>Sminthurinus</i>		14	2.3	3.8	53	2
3	<i>S. curviseta</i> - no competition		72	6.2	3.5	252	3
4	<i>S. curviseta</i> - <i>S. caeca</i>		54	3.1	5.2	280	4
5	<i>S. caeca</i> - no competition		43	2.5	5.4	232	8
6	<i>S. caeca</i> - <i>S. curviseta</i>		20	1.9	5.2	104	9
7	<i>F. candida</i> - no competition		58	4.8	3.0	174	5
8	<i>F. candida</i> - <i>H. matura</i>		44	3.1	4.3	189	6
9	<i>F. candida</i> - <i>S. caeca</i> & <i>curviseta</i>		26	3.1	1.5	39	7
10	<i>H. manubrialis</i> - no competition		72	5.2	3.8	274	10
11	<i>H. manubrialis</i> - <i>F. candida</i>		103	7.8	3.5	360	11

marizes this data for some of the most critical interactions. In all these cultures inaccuracy of counts at very large numbers was so great that an arbitrary maximum of two hundred was placed on any single reproduction. This eliminated gross inaccuracy as a result of a single inflated count. It should be noted that competitive interactions 2, 4, 6, and 8 bear many similarities. None shows any striking decrease in reproductive frequency compared to monospecific cultures under the same conditions, thus arguing strongly against spermatophore destruction or toxification of the substrate, or general oviposition inhibition, since all of these should have resulted in

lowering of this parameter. This leaves either egg destruction and/or oviposition interference. In three of the four cases (interactions 2, 4, and 6) there is a compensatory increase in the frequency of oviposition which would favor the latter hypothesis. Furthermore, if the reproductive interactions are broken up by the age of the colonies (see Table VI) it can be seen that all

TABLE VI

Interaction	Average number young per (recruitment) reproduction	Average reproductive rate in colonies reproducing	Reproductive frequency	Average productivity, all cultures participating	Number cultures active	Number reproductions	Intervals of days from start
1) <i>Arrhopalites caecus</i>	38	8.27	1.86	70	7	13	0-80
no competition	45	1.15	1.00	45	6	6	80-140
2) <i>Arrhopalites caecus</i>	14	2.87	2.7	38	7	19	0-80
Comp: <i>Sminthurinus quadrimaculatus</i>	14	0.64	1.00	14	6	6	80-140
3) <i>Sinella curviseta</i>	64	6.3	1.59	102	17	27	0-80
no competition	91	2.5	1.08	95	11.5	12	80-140
.....	69	8.5	0.50	34	8	4	140-200
4) <i>Sinella curviseta</i>	63	4.7	2.66	169	6	16	0-80
Comp: <i>Sinella caeca</i>	41	0.6	1.05	43	5.7	6	80-140
.....	43	0.6	1.33	57	3	4	140-200
5) <i>Folsomia candida</i>	46	5.4	1.33	62	18	24	0-80
no competition	84	3.5	0.87	73	11.5	10	80-140
.....	60	4.5	0.60	36	10	6	140-200
6) <i>Folsomia candida</i>	49	4.6	1.40	67	10	14	0-80
Comp: <i>Hypogastrura manubrialis</i>	43	1.7	1.90	81	5.8	11	80-140
.....	16	0.9	0.63	10	3.2	2	140-200
7) <i>Folsomia candida</i>	18	5.3	0.56	10	9	5	0-80
Comp: <i>Sinella caeca</i> or <i>curviseta</i>	21	0.9	0.50	10	8	4	80-140
.....	55	2.1	0.37	20	5.4	2	140-200
8) <i>Sinella caeca</i>	48	4.8	1.2	58	5	6	0-80
no competition	48	1.8	2.9	137	3.5	10	80-140
.....	15	0.3	1.0	15	3	3	140-200
9) <i>Sinella caeca</i>	21	3.2	2.25	47	8	18	0-80
Comp: <i>Sinella curviseta</i>	16	0.4	1.7	28	7.5	13	80-140
.....	27	1.0	0.75	20	4	3	140-200
10) <i>Hypogastrura manubrialis</i>	56	5.38	1.90	107	11	21	0-80
no competition	137	3.28	0.79	109	6.3	5	80-140
.....	150	0.75	0.40	60	5	2	140-200
11) <i>Hypogastrura manubrialis</i>	99	8.8	2.00	198	9	18	0-80
Comp: <i>Folsomia candida</i>	120	2.5	0.43	49	4.6	2	80-140
.....	150	1.8	0.25	38	4	1	140-200

four groups show a higher oviposition frequency during the first eighty days than comparable monospecific cultures. The fact that these changes cannot be attributed to the changing density of the first species of each interaction can be seen by examining Table VII. Here we can see the relative frequency of different population densities during the three time intervals. Comparison with tables 3 and 6 shows that changes in competitive populations cannot be correlated with these frequencies. Thus the hypothesis which appears to best fit our data is that in these four interactions the competitive

TABLE VII

Percentages of different population densities of first named species in different interactions during different time intervals.

Interaction number	population density								
	0-25	26-100	>100	0-25	26-100	>100	0-25	26-100	>100
1	66	34	0	60	40	0	80	20	0
2	50	50	0	50	50	0	50	50	0
3	33	29	38	29	19	52	0	0	100
4	17	17	66	20	0	80	20	40	40
5	54	29	17	41	22	37	25	50	25
6	60	10	30	27	27	56	23	39	38
7	58	42	0	62	25	13	33	45	22
8	50	33	17	17	33	50	25	25	50
9	43	57	0	29	57	14	0	75	25
10	55	25	20	65	6	29	30	50	20
11	10	30	60	22	33	45	0	50	50
Time interval (days from start)	0-80			80-140			140-200		

mechanism involves primarily a reduction in the number of eggs laid at one time. A somewhat different picture is to be seen in interaction 9 (see table V). Here all aspects of reproduction by *F. candida* are adversely affected by the presence of significant numbers of *Sinella*. This is reflected by the extremely low average productivity. This represents a candid disaster which could be the result of several superimposed inhibitory mechanisms. Interaction 11, where *Hypogastrura manubrialis* had *Folsomia candida* as a competitor is at first glance most confusing. It appears that *Folsomia* stimulates the development of *H. manubrialis* in every respect, yet the normal result is

the eventual extinction of *H. manubrialis*. If, however, you examine table 6 again, you will note that this stimulation involves only the early period of culture growth and that during the latter periods *Folsomia* probably has an inhibitory effect. The probability that presence of small numbers of competitors has a stimulatory effect upon population growth in general has already been discussed and thus the early stimulation of *Hypogastrura* by *Folsomia* appears to be merely an exaggeration of the normal phenomenon. In interaction 11, the most striking inhibitory effect in older cultures appears to be a lowering in reproductive frequency. This would match up well with inhibition through toxification of the substrate, and is further supported by the fact that the growth curves in this interaction most nearly match the dropping type which would be expected in such a case (see graph 2). It should be noted that there are similar though less pronounced drops in non-competitive cultures. Thus it appears probable that the eventual destruction of *Hypogastrura* in mixed culture with *Folsomia* may be the result of substrate toxification both by its own species and by *Folsomia*.

In short, then, the inhibitory mechanisms appear to differ in different interactions. In a number the presence of one species seems to prevent effective reproduction in the other species. In most cases where both species breed, some form of oviposition interference appears to be probable, possibly combined with destruction of eggs. The inhibitory action of *Sinella* upon *Folsomia candida* appears to be general, probably involving the superposition of several mechanisms. The competitive effect of *Folsomia* upon *Hypogastrura* appears to be mediated by some form of toxification analogous to the feedback mechanisms reported in amphibia by Richards in 1958 and Rose in 1960. At lower densities it appears that in all cases the presence of competitors has a stimulatory effect upon reproduction. The most general inhibitory mechanism then would appear to involve some sort of social interaction.

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Note

Because of the very large number of cultures studied, individual culture graphs are shown only for those cultures considered to be of critical importance. Data concerning the remainder is available on request.

SUMMARY

The effect of interspecific competition upon the growth of collembolan populations in standard culture jars with excess food was studied for thirteen interspecific interactions involving eleven species. Three basic types of result were found. In most interactions one species dominated clearly, either preventing reproduction in the second species or quickly eliminating it once reproduction had occurred. In four cases one species was initially dominant but was normally replaced by the second species as cultures developed. In one case no clear dominance was displayed and the two species appeared to be able to exist indefinitely in mixed culture. These two species were closely related both taxonomically and ecologically.

Six competitive interactions were tested under four different conditions of temperature and light fluctuation. Regular strong fluctuations in light and temperature virtually blocked reproduction in all species. Other differing conditions did not significantly alter the results of the experiments except for the interaction between *Hypogastrura* and *Arrhopalites* where regular temperature fluctuation reversed the normal competitive outcome.

Analysis of all the data showed a distinct inhibitory effect of increased competitor numbers which could not be explained on a basis of crowding. In addition, this was an indication that small numbers of competitors had a stimulatory effect on the reproduction of the first species.

Possible mechanisms for the reproductive inhibitions were analyzed and it was concluded that the mechanisms differed with the interaction, with oviposition interference being the most common mechanism.

RÉSUMÉ

La concurrence entre espèces mesurée par l'accroissement des populations de collemboles dans des bocaux de culture avec suraliments, a été étudiée selon treize types d'actions réciproques concernant onze espèces. On a mis en évidence trois types fondamentaux de réactions. Dans la plupart des actions réciproques une espèce dominait nettement, soit en empêchant la reproduction de la deuxième espèce soit en l'éliminant rapidement aussitôt que la reproduction s'était produite. Dans quatre cas une espèce dominante au début fut remplacée normalement par la seconde espèce à mesure que les cultures se développaient. Dans un cas aucune prédominance nette ne s'est manifestée et les deux espèces paraissaient pouvoir coexister indéfiniment en culture mixte. Ces deux espèces étaient apparentées étroitement aussi bien taxonomiquement qu'écologiquement.

Six actions réciproques concurrentes furent suivies dans quatre conditions différentes de température et de fluctuation de la lumière. De fortes fluctuations régulières de la lumière et de la température ont bloqué la reproduction dans toutes les espèces. D'autres conditions différenciées n'ont pas modifié d'une manière significative les résultats des expériences sauf pour l'action réciproque *Hypogastrura-Arrhopalites*.

L'analyse de toutes les données recueillies a démontré un net effet inhibiteur qui ne peut s'expliquer sur la base du simple entassement d'individus de plus en plus nombreux. De plus, il apparaît que des concurrents même peu nombreux peuvent avoir un effet stimulant sur la reproduction de la première espèce.

Parmi les mécanismes possibles pour expliquer les inhibitions ou les dominances successives, il semble que le plus fréquent soit une inhibition de l'oviposition.

ZUSAMMENFASSUNG

Der Einfluss zwischenartlicher Konkurrenz auf die Vermehrung von Collembolen-Populationen wurde in 13 Fällen interspezifischer Einwirkung, an denen 11 Arten beteiligt waren, untersucht. Die Tiere wurden in Standard-Zuchtgefäßen bei Ueberernährung gehalten. Drei grundlegende Arten von Ergebnissen wurden erzielt. In den meisten Fällen zwischenartlicher Einwirkung war eine Art klar vorherrschend und verhinderte die Fortpflanzung der zweiten Art oder verdrängte diese schnell, nachdem die Fortpflanzung einmal erfolgt war. In vier Fällen war eine Art anfangs dominierend, wurde aber im Laufe der Entwicklung der Zucht auf natürliche Weise von der zweiten Art abgelöst. In einem Fall konnte keine eindeutige Vorherrschaft beobachtet werden und die beiden Arten schienen unbegrenzt in gemischter Zucht leben zu können. Diese beiden Arten waren sowohl taxonomisch wie ökologisch eng verwandt.

-- Sechs Konkurrenzeinwirkungen wurden unter vier verschiedenen Bedingungen mit unterschiedlichen Temperatur- und Lichtschwankungen untersucht. Regelmässige starke Licht- und Temperaturschwankungen verhinderten grundsätzlich die Fortpflanzung bei allen Arten. Andere abweichende Bedingungen änderten nicht wesentlich die Ergebnisse der Experimente, mit Ausnahme der Wechselwirkung zwischen Hypogastrura und Arrhopalites, wo regelmässige Temperaturschwankungen das normale Konkurrenzergbnis umkehrten.

Die Analyse sämtlicher Ergebnisse zeigte eine deutliche Hemmwirkung bei einer grösseren Anzahl von Konkurrenztieren, welche nicht durch Uebervölkerung zu erklären war. Dies war ein zusätzlicher Hinweis darauf, dass eine kleine Anzahl von Konkurrenztieren einen stimulierenden Einfluss auf die Fortpflanzung der ersten Art ausüben.

Die möglichen Mechanismen der Fortpflanzungshemmung wurden untersucht und wir kamen zu dem Schluss, dass die Mechanismen je nach zwischenartlicher Einwirkung verschieden sind, wobei die Verhinderung der Eiablage der am häufigsten zu beobachtende Mechanismus ist.

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